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Evaluation of ecosystem responses to land-use change using soil quality and primary productivity in a semi-arid area, Israel

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A B S T R A C T

Land-use change (LUC) from natural to human-dominated land is a critical aspect of global change and ecosystem response. To improve our understanding of LUC, this study focused on: (1) developing a general theoretical framework for quantifying and evaluating the attributes of ecosystem response as a consequence of LUC; and (2) testing the validity of this framework using recent LUC in the desert fringe of the northern Negev Desert. Our framework is based on the premise that changes in soil and vegetation states are the most important and universal facets of ecosystems' response to LUC. The framework depicts LUC as trajectories of indicators that signify soil and vegetation states, such as the soil quality index (SQI) and aboveground net primary productivity (ANPP), respectively, in a phase plane. The trajectories are characterized by both magnitude and the direction of the change that enable us to address and compare the general trends of the LUC. Our study explored the validity of the proposed framework for the following LUC cases: (1) grazing to natural ecosystem; (2) natural to grazing ecosystem; (3) rain-fed agricultural to natural ecosystem; and (4) rain-fed agricultural to grazing ecosystem. The SQI was quantified by 14 physical, biological, and chemical attributes that were merged into one index, while the ANPP was derived from biomass sampling. All transitions show strong relationships between SQI and ANPP ($0.70 < R^2 < 0.85$; $p < 0.05$). Transitions from grazing to natural ecosystems are characterized by an increase in both SQI and ANPP variables; while all transitions that change from agricultural systems to less intensively managed systems, such as grazing or a natural system, show no change or a decrease in both SQI and ANPP. We infer that all the trajectories' trends are a result of changes in the biodiversity dimensions during LUC. Analysis of the results revealed four properties of a theoretical framework that can be used for the developing science of LUC and ecosystem responses. Our framework enables: (1) a comparison between different types of LUC; (2) a study of transitions among self-organized and managed ecosystems; (3) the identification of short- and long-term effects; and (4) the integration of biodiversity and ecosystem function. We suggest that the four properties of the framework can provide the foundation for the development of an LUC science. However, the validity and the generality of the framework should be tested over a wide range of LUCs of terrestrial systems in the world.

1. Introduction

1.1. Land use changes: Conceptual framework

The term land use encompasses a wide range of human activities on the land surface, such as grazing, agriculture, and urban use (DeFries et al., 2004). Land-use activities, whether converting natural landscapes to human use or changing management practices on human-dominated lands, have transformed a large proportion of the planet's land surface (Foley et al., 2005). Worldwide observations have confirmed that a large portion of the terrestrial surface has been changed from natural ecosystems to human-dominated ecosystems, mainly to grazing and agro-ecosystems (e.g. Goldewijk, 2001; DeFries et al., 2004; Foley et al., 2005; Zhou et al., 2006; de Chazal and Rounsevell, 2009). The transitions in land-use activities are largely due to demographic and economic causes and are expected to increase over time. Different parts of the world are at different transition stages, depending on their history, social and economic conditions, and ecological context. The type of land-use change (LUC) significantly affects key aspects of

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ecosystem responses, in terms of ecosystem structures, functions, and dynamics, and creates new complex interactions among soil, nutrients, and vegetation that determine the ecosystem health (Adeel et al., 2005). These responses vary not only according to the state of LUC, but also with the biophysical and ecological setting (DeFries et al., 2004; Foley et al., 2005) due to the modifications of biodiversity, productivity, and soil quality (Matson et al., 1997; Tscharntke et al., 2005).

Historically, LUCs of natural environments to rangelands and, later, to croplands are known from the beginning of human settlement as a consequence of the domestication of plants and animals, and of land cultivation, and this type of ecosystem transformation became the most common on earth (Goudie, 2009). During the last 300 years, the global area of agricultural land has increased from 256 Mha in 1700 to 1471 Mha in 1990, and it currently occupies between 24% and 38% of the Earth's land surface (Goldewijk, 2001; Swinton et al., 2007). In addition, the global amount of pasture land has also increased from 524 Mha in 1700 to 3451 Mha in 1990, and it occupies around 25% of the global land surface (Asner et al., 2004).

Previews studies show the important role of ecosystem response to LUC due to modulation of the biosphere by changes in biogeochemical, biodiversity, hydrological, and climatic responses (e.g. DeFries et al., 2004). However, more theoretical and empirical work is needed in order to manage these human-controlled biospheres (Foley et al., 2005). Land use change models that incorporate ecosystem processes, dynamics, and responses can help to advance our understanding of the ecosystem-level consequences of LUC and their sustainable management. In this study, we aim at: (1) developing a theoretical framework for evaluating the changes of ecosystem response to LUC; and (2) demonstrating the validity of the framework using LUCs in the northern Negev Desert as a case study. We propose that the transitions between natural, grazed, and agricultural ecosystems, which include the human activities of land cultivation and replacement of the natural vegetation and animals by domesticated organisms (Tscharntke et al., 2005; Swinton et al., 2007) are the prevailing LUC on earth, and can be presented by a simple state and transition conceptual scheme. This scheme can be quantified in relation to changes in soil and vegetation states or other core states, such as biodiversity, hydrological, and climate (Fig. 1). The scheme includes three ecosystems: (1) Natural – defined as self-organized systems without human management (Levin, 1998) or livestock grazing (Perevolotsky, 1999). In our framework, abandoned agricultural and grazing systems that are self-organized by plant and animals' re-colonization from the available natural species pool are natural ecosystems; (2) Grazing – defined as terrestrial ecosystems with high densities of domestic livestock herbivores introduced by humans. The abundant domestic herbivores determine plant community dynamics and ecosystem processes (Manley et al., 1995; Greenwood and McKenzie, 2001; Lin et al., 2010); (3) Agricultural – defined as an ecosystem under intensive cultivation aiming at the production of crops. These agricultural management reduce the species diversity and the complexity of species assemblages, energy flow, and nutrient fluxes in the system (Clergue et al., 2009).

1.2. Ecosystem responses to land use changes

We further propose that reciprocal LUCs between the above three states are possible and create six types of transitions (Fig. 1): (1) Transition from natural to grazing ecosystem. This transition occurs mainly in natural grasslands, shrublands, and savannas since domesticated grazing livestock are typically adapted to these biomes. The transition is maintained by managing the stocking rates and foraging strategies of the domestic animals (Dean and Macdonald, 1994; Manley et al., 1995). (2) Transition from natural to agro-ecosystems. This transition is continuously sustained by human management that includes the clearing of native vegetation and its replacement by domesticated plant and animal species whose ecological traits are controlled by humans (Swift et al., 2004; Clergue et al., 2009; Smith et al., 2012). (3) Transition from agro-ecosystems to natural ecosystems. This transition occurs as a result of the abandonment of agricultural fields where natural processes of self-organization facilitate the natural regeneration of ecosystem structure, function, and processes and are preserved by natural succession and disturbance regimes (MacDonald et al., 2000). (4) Transition from grazing to agro-ecosystems. This transition takes place when socio-economic conditions inhibiting access to input factors, such as water and fertilizers, are removed. The human management includes the input of energy and nutrients to the system (Metzger et al., 2006; Goldstein et al., 2012). (5) Transition of agro-ecosystem to grazing ecosystems. This transition takes place when socio-economic conditions are poor or when the environmental conditions are not profitable for agricultural production, and it persists under continuous management by humans that includes the abandonment of agricultural land and the introduction of domestic livestock. (6) Transformation of grazing to natural ecosystems. This transition takes place when conservation efforts to restore the natural environment take place in order to prevent degradation and desertification processes. For example, this transition can be created by excluding livestock from the grazing system for allowing the recovery of the natural vegetation (Perevolotsky, 1995, 1999). This transition encourages natural processes of self-organization that facilitate the regeneration of the natural ecosystem structure, function and processes.

Changes in soil and vegetation states are important facets of ecosystem response to LUC (DeFries et al., 2004; Foley et al., 2005). Therefore, we propose that a trajectory of variables that represent soil and vegetation states, along with their relations, can be used as a common currency to describe substantial changes of terrestrial ecosystem components due to LUC, to address general trends, and to analyze effects on ecosystem structure (e.g., soil quality) and functions (e.g., primary production) (Fig. 2). We suggest a conceptual framework for the trajectories in the soil and vegetation states phase plane resulting from LUC: (1) Trajectories that signify similar (equal contribution of the two variables) relationships between the two states. These trajectories are marked by the diagonal line that indicates either a common increase or a decrease in both variables. We assume that the contribution of each variable changes between the trajectories due to different effects of soil and vegetation relations. These relations are the most prevailing trajectories since, in natural, grazed, and agricultural ecosystems; the capacity of the soil to produce plant biomass (productivity function) is an essential function. This capacity is determined by the soil state. Under high soil quality, within a natural or managed ecosystem, the ability to sustain plant and animal productivity is high (Karlen et al., 1997). However, when soil is degraded and soil quality is low, the ability to support primary productivity is low; (2) Trajectories that signify changes in either the soil or vegetation state but not simultaneously in both. These trajectories are marked by the horizontal and vertical lines in the phase plane and indicate either an increase or a decrease in only one state variable. We propose that an increase or a decrease in the vegetation or in the soil state, for example, occurs when the environmental factors (landscape quality factors) are not uniform as temperature, topography, and hydrology, or is due to ecological processes, such as herbivores. This framework can present diverse trajectories due to different relations between vegetation and soil states. The trajectories that emphasize equal contributions or signify changes in soil or vegetation states only represent under extreme conditions and all other relations can exist in reality. The magnitude and the direction of the trajectories enable us to address and compare general trends of change in ecosystem attributes and responses as a result of LUC.

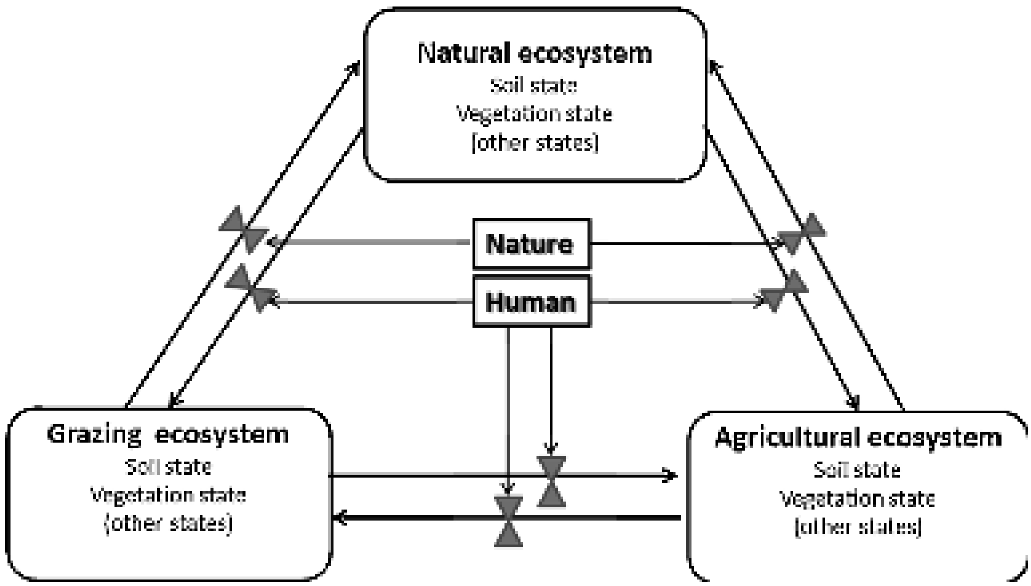

Fig. 1. Conceptual framework of ecosystem response to land-use changes. The conceptual scheme shows the relationships between natural, grazing, and agricultural ecosystems governed by natural and human processes. Each ecosystem is mainly defined by soil and vegetation states but can also be defined by other core states, such as hydrological, biodiversity, climatic and bio-geophysical states. There are six possible transformations among ecosystem states; two are controlled by natural processes and four by human interventions.

This framework suggests diverse trajectories of the soil and vegetation state phase plane by studying the magnitude and direction of the trajectories.

We tested the utility of the above conceptual framework (Fig. 2) in relation to four LUCs that recently occurred in the Negev Desert, Israel. The phase plane is based on soil and vegetation states. We used the soil quality index (SQI) as an indicator to assess the soil state and aboveground net primary productivity (ANPP) to appraise the vegetation state. Soil quality controls soil functions that regulate the two basic ecosystem processes of energy flow and nutrient cycling (Acton and Padbury, 1993; Brejda et al., 2000; Bastida et al., 2008). Soil quality, by definition, reflects the capacity to sustain plant, animal, and microbial productivity, and therefore to promote abiotic and biotic interactions that are the core of ecosystem processes (Herrick, 2000; Riley, 2000). Soil quality involves physical, biological, and chemical properties that are merged together to indicate the soil functioning that determines an ecosystem's state (Andrews et al., 2002; Gugino et al., 2009). The capacity of soil to sustain ecosystem processes is a function of intrinsic soil properties and extrinsic factors (e.g., precipitation, temperature, topography, and hydrology) (Carter, 2002). The sustainability of ecosystem processes and responses, in particular nutrient cycling, directly depends on the soil structure and function. Soil state is, therefore, a decisive factor for a broad range of patterns and processes in ecosystems, including bio-productivity, biodiversity, stocks and flows of elements, food webs and water flows, as well as ecosystem resilience (Holling, 1973).

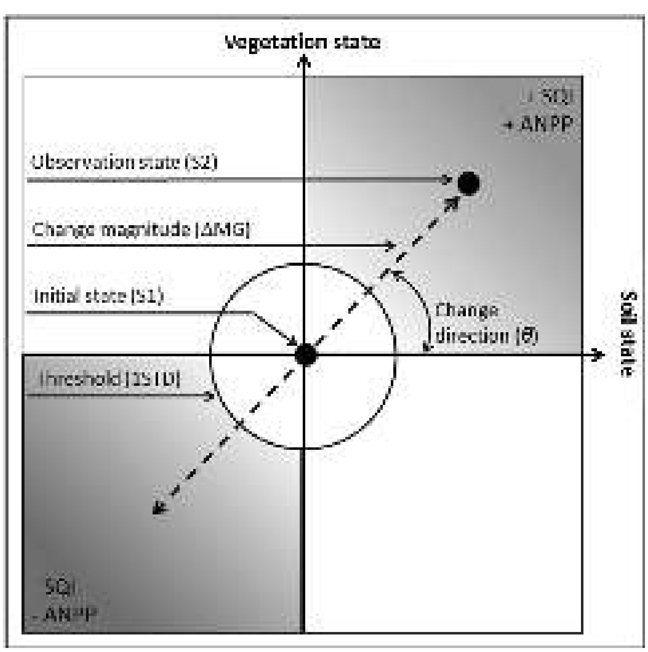

Fig. 2. Conceptual scheme based on soil quality index (SQI) and aboveground net primary productivity (ANPP) as indicators for quantifying ecosystem response to land-use changes (LUCs). Dashed arrows indicate specific possible directions and magnitudes of LUC. The length of the arrow indicates the magnitude of change, and slope angle represents the relative changes between the vegetation and soil states. S_1, initial state; S_2, observed states, threshold represents significant differences between the initial state and the observed state.

In addition to changes in the soil state, LUC can result in changes in the vegetation state, emerging from changes in soil quality but also from changes in ecological processes, such as competition and herbivores (e.g. Coughenour, 1991; Marc and Mazumder, 1998; Greenwood and McKenzie, 2001; Asner et al., 2004; Bisigato et al., 2005; Lin et al., 2010). A change in the vegetation state usually induces changes in biomass flows that can be evaluated using ANPP as a prominent ecological indicator of ecosystem response to LUCs that are controlled by natural and human ecosystems. ANPP is a primary variable of ecosystem functioning (Whittaker and Likens, 1997) that determines the amount of trophic energy available for transfer from plants to other levels in the trophic webs of ecosystems (Vitousek et al., 1986; Kay et al., 1999; Gaston, 2000; Erb et al., 2009). ANPP is strongly interlinked with ecosystem intactness by the provision of energy to all ecosystem components. The alteration of ANPP by LUCs strongly influences biodiversity that, in turn, affects the ecosystem state (Erb et al., 2009).

In this study, we evaluate two ecosystems: (1) a grazing system that includes a short-term (about 20 years ago) LUC to an area where the grazing has been excluded after a long-term pastoralism land-use (for about 10,000 years) (Noy-Meir and Seligman, 1979); and (2) an agricultural ecosystem that was transformed about 20 years ago either to a natural ecosystem (abandoned agriculture) or to a grazing ecosystem after short-term (about 40 years ago) agricultural management. We assume that the time scale of the land use before transition and the time scale of the transition are important in controlling the dimensions of the trajectories in the phase plane. Specifically, we focus on the following four transitions: (1) a grazing ecosystem to a natural ecosystem; (2) a natural ecosystem to a grazing ecosystem; (3) an agro-system to a natural ecosystem; and (4) an agro-system to a grazing ecosystem. We tested the framework in relation to the magnitude and direction of the trajectories within the phase plane of SQI and ANPP in the four LUCs. Direction refers to whether trajectories signify a positive or negative relationship between SQI and ANPP, quantified by the angle of the trajectory, and the magnitude refers to the relative change (Fig. 2).

We generated four testable hypotheses, related to the Negev Desert, using the conceptual framework (Fig. 2) as a basis for the quantification of ecosystem response to LUC. The first hypothesis suggests that during transitions from a grazing to a natural ecosystem, the trajectories will show a positive relation in both SQI and ANNP. This is based on the assumption that grazing, in the long run, negatively affects both ANPP and SQI (Goudie, 2009). The effect of grazing on soil is mainly caused by trampling and the compaction of the soil, and its effect on vegetation is mainly seen in the uptake of biomass (Warren et al., 1986; Greenwood and McKenzie, 2001; Zaady et al., 2001; Lin et al., 2010). We suggest that excluding grazing from a system, even for a short period, enables the development of a diverse plant community and, consequently, increases primary production (Osem et al., 2002, 2004, 2006). We also assume that soil surface properties will recover over time (Greenwood and McKenzie, 2001). We suggest that the recovery rate of the vegetation is higher than that of the soil. This will affect the direction of the change with a steeper angle (>45°) toward the ANPP. The magnitude of trajectory in the phase plane will be relatively short since 20 years is a short period for the transition toward a natural system after a long-term persistence of a pastoral system. The second hypothesis suggests that the transition from a natural to a grazing system shows a trend opposite to the trajectory suggested in the first hypothesis. This is based on the assumption that introducing livestock to a natural system increases resource uptake and soil degradation (Fleischner, 1994; DeFries et al., 2004). The third hypothesis refers to the transitions from agricultural to natural systems. In our case study the agriculture system is rain-fed agriculture that does not receive any fertilization. Here we suggest that the directions and magnitudes of the trajectories show changes in both SQI and ANPP that show a positive relation that indicates an increase in both indicators. This is based on studies showing that abandoned agriculture allows the re-colonization of species from the natural area, thus increasing biodiversity, productivity, and soil quality (e.g. Swift et al., 2004; Clergue et al., 2009; Idowu et al., 2009; Smith et al., 2012). As we propose in the two previous hypotheses, in this case, the recovery time of the vegetation will be longer than the soil recovery, resulting in a steep slope angle (>45°). The length of the trajectory is relatively short due to the short period of LUC from agricultural to natural ecosystems. The fourth hypothesis refers to the transition from an agricultural to a grazing ecosystem. We propose that in this case, no changes will be observed in either SQI or ANPP. This is based on the assumption that LUC from one exploitative system to another will preserve the degraded state of the system (DeFries et al., 2004).

Testing these hypotheses enables us to address a general question relating to LUC and ecosystem responses – do natural ecosystems have higher SQIs and ANPPs than agricultural and grazing ecosystems? In addition, we can tackle three specific questions relating to the semi-arid northern Negev Desert: (1) how do LUCs between grazing, natural, and agricultural ecosystems affect SQI?; (2) how do LUCs between grazing, natural, and agricultural ecosystems affect the ANPP of herbaceous vegetation?; and (3) what are the specific effects of LUCs between natural, grazing and agricultural systems on the relations between SQI and ANPP trajectories?

2. Study sites

The study areas are located in long-term ecological research (LTER) sites in the northern Negev Desert of Israel, in the semi-arid transition zone between the Mediterranean and the arid zones (Shachak and Groner, 2010). In this study, we evaluate two different ecosystems – grazing and agricultural systems.

2.1. Grazing system

The study site of the grazing system was located at the Lehavim experimental farm in the northern Negev region of Israel (31°21N, 34°49E) at an altitude of about 250–500 m a.m.s.l. The average annual precipitation is 305 mm, mainly between December and March. The average daily temperature ranges from 10 °C in the winter to 25 °C in the summer (Osem et al., 2002). The bedrock lithology is of Eocene chalk, and the soil texture is loamy (Osem et al., 2004, 2006). The landscape is a shrubland with a two-phase mosaic of shrub patches and open soil patches. The physiognomy in the study area is shrubs, with *Sarcopoterium spinosum*, *Coridothymus capitatus*, and *Thymelea hirsute* as the dominant species. Annual species represent 56% of the regional flora (Danin and Orshan, 1990). The herbaceous vegetation appears in the mid-winter after the rainfall begins and persists for 2–5 months, depending on the amount and distribution of rainfall.

The 800-ha farm was established in 1980 and, since then, has been moderately grazed by flocks of sheep and goats, under the auspices of the Israeli Ministry of Agriculture and Rural Development. The area is grazed every year by a flock of about 600 Awassi sheep and 200 goats, starting in late January, after rainfall onset and plant establishment, and continuing until May (green pasture), and again from August to December (dry pasture). A shepherd directed the flock over the range, to ensure foraging over the entire area and maximal consumption of available vegetation. Four permanent enclosure plots (10 m × 10 m) were established on each slope in 1993 to prevent sheep and goat grazing. These plots were near the wadi (dry stream) shoulders where the slope is moderate (Supplementary data 1; Fig. 3).

2.2. Agricultural system

The study of the agricultural system was carried out at the Migda experimental farm located in the semi-arid northern Negev region of Israel (34°25E, 31°22N), northwest of Beer-Sheva at a mean altitude of about 100–120 m a.m.s.l. The average annual rainfall is 250 mm; most of the precipitation occurs between December and March. The average daily temperature ranges from 10 °C in the winter to 27 °C in the summer. The growth season is from November to April, during the rainy period, mainly of rain-fed wheat. The soil is sandy-loam 1–2 m deep. The farm was established in 1960 by the Agricultural Research Organization for extensive agriculture research that includes grazing under different grazing regimes, combining agricultural, mainly wheat, production, and grazing in rotation.

The area is grazed by a flock of about 800 Awassi sheep and 600 goats on the stubble in two periods – the first after wheat is harvested for hay between late February and May (green pasture), and the second at the end of the growing season after wheat is harvested for grains between June and October (dry pasture) (Bonfil et al.,

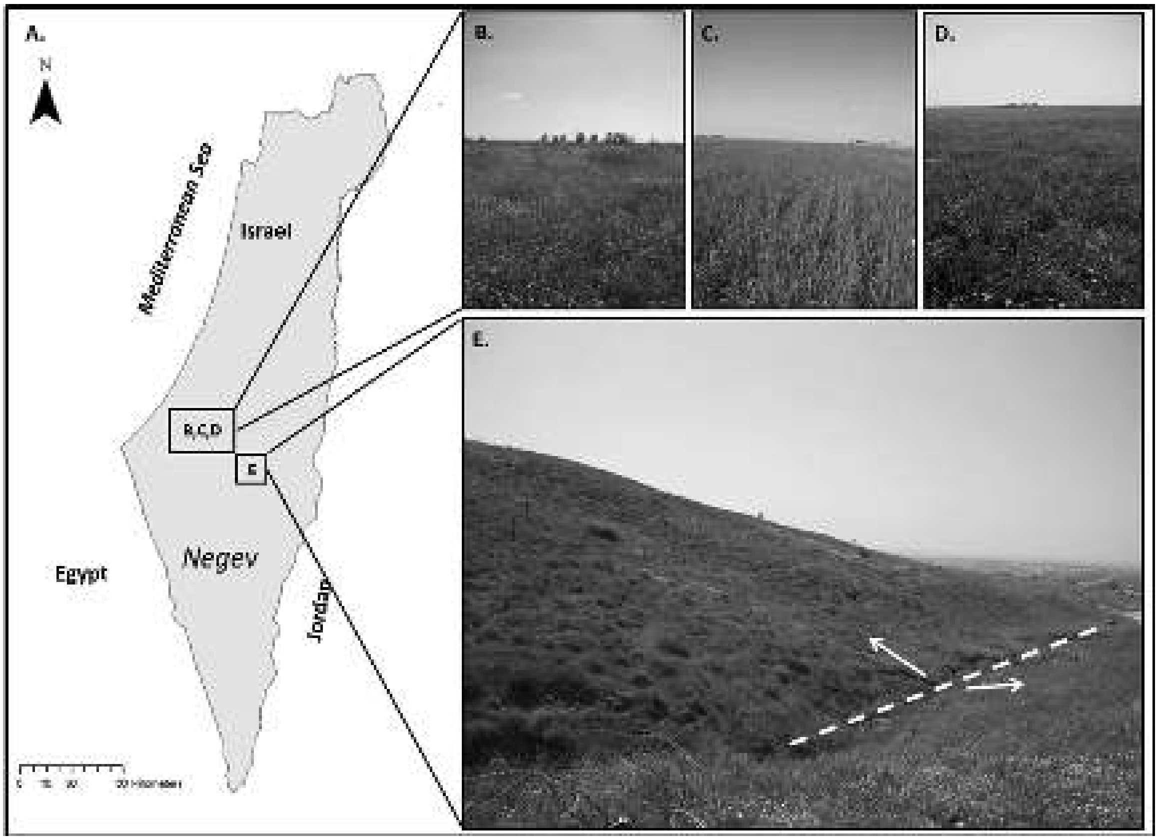

Fig. 3. (A) Two main study sites in the northern Negev Desert with rainfall isohyets; (B) natural system – an abandoned field with no grazing at Migda Farm; (C) an agricultural wheat field with moderate grazing at Migda Farm; (D) a grazing system – abandoned field with moderate grazing at Migda Farm; and (E) a grazing system at the Lehavim study site along the north- and south-facing slopes.

2004). The grazing at the farm is managed by controlling the intensity, stocking density, flock size, and timing of herd introduction in the field. Three rain-fed fields were examined in this study: (1) an abandoned agricultural field in an area of 5 ha of mainly natural annual vegetation where no cultivation, fertilization, or grazing was performed; (2) an abandoned field with grazing in an area of 9.6 ha, mainly with annual vegetation with grazing, but with no cultivation or fertilization; and (3) a monoculture agro-pastoral (agricultural combined with grazing management in rotation) wheat field in an area of 9.5 ha, with cultivation but with no fertilization, and with moderate grazing between crop production seasons (Supplementary data 1; Fig. 3).

3. Methodology

3.1. Experimental design and sampling

The experiment was performed at the two above mentioned farms with different LUCs with four transitions. The sampling design in the grazing systems was based on the different grazing treatments and included five replicates of 1 m^2, randomly selected in each treatment: (A) a natural system along the south-facing slope with no grazing; (B) a grazing system along the south-facing slope with moderate grazing; (C) a natural system along the north-facing slope with no grazing; and (D) a grazing system along the north-facing slope with moderate grazing. The sampling in the agricultural system experiment farm included: (E) a natural system in an abandoned agricultural field with natural vegetation and no grazing; (F) a grazing system in an abandoned agricultural field with natural vegetation with grazing; and (G) an agro-system in the agro-pastoral wheat field with moderate grazing ($n = 35$ replicates of 1 m^2 quadrats). The sampling of the soil in each replicate included four soil samplings (four repeated measurements for each replicate). The sampling of the ANPP in each replicate included nine aboveground biomass samplings in a sub-quadrate of 33 cm^2 (nine repeated measurements for each quadrate).

3.2. Soil sampling processing and analysis

3.2.1. Soil sampling and analysis

Soil samples were collected in late August of 2011, at a depth of 0–0.15 m, at the peak of the dry season. The sampling was conducted following a stratified random sampling based on an experimental design as mentioned above ($n = 35$ replicate of 1 m^2 quadrats). In each replicate, four soil samples of 700 g were collected, for a total of 140 soil samples. All dry soil samples were transferred to the laboratory and were stored unopened until analysis. The Cornell Soil Health Test (CSHT) protocols were adopted for analyzing 14 physical, biological, and chemical soil properties (Idowu et al., 2008; Schindelbeck et al., 2008; Gugino et al., 2009). The physical properties included soil texture (fractions of clay, silt, and sand), wet aggregate stability (AGG), available water content (AWC), surface hardness (SH), and hydraulic conductivity (HC). The biological properties included soil organic matter (SOM), potential active carbon (PAC), and root health (RH). The chemical properties included pH, electrical conductivity (EC), extractable phosphorus (P), extractable potassium (K), extractable ammonium (NH_4^+), and extractable nitrate (NO_3^-). All laboratory measurements were carried out with CSHT's standards. However, minor modifications were introduced due to the specific management practices, climatic regions, and available tools including: (1) wet aggregate stability that was measured by an aggregate stability kit (Herrick, 2000);

(2) available water content (AWC)) that indicated the soil moisture (Black, 1965); (3) NH_4^+ and NO_3^- that was measured by potassium chloride extracts (Stevenson, 2005); and finally (4) hydraulic conductivity property that was measured by a mini-disk infiltrometer in the field (Ankeny et al., 1991). The soil texture, which is a composition of three fractions clay, silt, and sand, is not a quality variable and therefore is not included in the SQI. However since the soil texture contributes to the inherent soil quality and the characteristic of the soil is derived from soil forming processes; these characteristics are difficult to be changed through management.

3.2.2. Soil quality index

Evaluation of the soil quality was carried out using the general approach of the soil quality indices, involving scoring functions for each of the above mentioned soil properties (Andrews et al., 2004). The scoring functions were defined in a simple nonlinear polynomial framework. Each soil property was transformed through a scoring algorithm into a unitless score (0–1) representing its quality in that system so that the scores may be combined to form a single value (Karlen et al., 1997, 2001, 2003; Andrews et al., 2004). The interpretation of the scoring function was then integrated into an index calculated by a principle component analysis (PCA) (Masto et al., 2007, 2008; Bhardwaj et al., 2011). The index values ranged from 0 to 1 where low values indicate poor soils while high values indicate healthy soils (Gugino et al., 2009).

The success and usefulness of this method depend mainly on setting the appropriate critical limits for individual soil properties. Threshold (optimum) values for each property can be obtained from a range of values measured in natural ecosystems and on the critical values from the literature, where soil functioning exhibits the potential soil functioning of the ecosystem (Glover et al., 2000; Arshad and Martin, 2002). After finalizing the thresholds, each soil property value was recorded by the different algorithms (scoring functions) to transform it to a unitless score Si, using the following equation (Masto et al., 2007, 2008; Kinoshita et al., 2012):

$$\mathrm{Si} = \left(1 + e^{-b(x-a)}\right)^{-1} \tag{1}$$

where x is the normally distributed soil property value, a is the baseline value of the soil property where the score equals 0.5 (inflection point) or the population mean of the natural ecosystems, and b is the slope tangent of the baseline curve. Three types of scoring functions were considered: (1) "more is better" – an upper asymptotic sigmoid curve (negative slope) that characterizes aggregation, residual water, soil organic matter, potential active carbon, ammonium, nitrate, and potassium; (2) "less is better" – a lower asymptote (positive slope) that characterizes root health and surface hardness; and (3) an optimum mid-point-Gaussian function that characterizes pH, EC, phosphorus, and hydraulic conductivity. The curve shapes were determined by the literature (Glover et al., 2000; Karlen et al., 2001, 2003; Andrews et al., 2004; Schindelbeck et al., 2008). All the soil property scores were integrated from the previous stage into a single additive index value termed a Soil Quality Index (SQI) (Eq. 2). This value is considered to be an overall assessment of soil quality, reflecting the management practice effects on soil function (Masto et al., 2007, 2008). To evaluate the index, the PCA statistical method, a common tool in chemometrics for data compression and information extraction, was used. A PCA finds the combinations of the soil's transformed properties that describe major trends in the data:

$$\mathrm{SQI} = \sum_{i=1}^{n} \mathrm{PWi} \times \mathrm{Si} \tag{2}$$

where PWi is the PCA weighing factor. Standardized PCAs of all (untransformed) data that differed significantly between treatments in the different LUCs were performed using the MATLAB package (Wise et al., 2006). The equation was normalized to get a maximum SQI with a score of one. Principal components (PCs) with eigenvalues higher than 1 that explained at least 5% of the variation of the data were examined (Andrews et al., 2002; Masto et al., 2008). Under a particular PC, only the variables with high factor loading were retained for soil quality index. High factor loading was defined as having an absolute value within 20% of the highest factor loading. When more than one variable was retained under a single PC, a multivariate correlation was employed to determine if the variables could be considered redundant ($R \geq 0.8$) and, therefore, eliminated from the SQI. If the highly loaded factors were not correlated, then each was considered important and, thus, retained in the SQI. Among well-correlated variables, the variable with the highest factor loading (absolute value) was chosen for the SQI. Each PC explained a certain amount of variation (percent) in the total dataset, and this percentage provided the weight for the variables chosen under a given PC.

3.2.3. Aboveground net primary productivity

The net primary herbaceous production provides a comprehensive evaluation of the ecosystem state, including measures of changes in ecosystem response to LUC (Running and Coughl, 1988; Running et al., 1995, 2004; Carter, 2002; TurHorst and Munguia, 2008). In the Negev, net primary herbaceous production can be determined by annual ANPP accumulation (Running and Coughl, 1988; Houghton, 1991, 2005; Fabricius et al., 2003; DeJong and Jetten, 2007). ANPP was estimated as the annual maximum plant biomass accumulation. Plant biomass was measured by quantifying the peak dry mass of plants per unit area in each treatment. Herbaceous vegetation aboveground biomass samples were collected three times during the peak of the growing season (April) in the years 2010, 2011, and 2012. The sampling was conducted in a stratified random method based on the experimental design. All the replicates were harvested in 0.33 m^2 sub-quadrats (nine repeated measurements for each quadrate); the total number of samples was 315 of aboveground biomass per year. The aboveground plant biomass was weighed, after a 48 h oven drying (75 °C). The ANPP values recorded by the algorithm of the "more is better" upper asymptotic sigmoid curve (Eq. 1) were transformed to unitless scores (Masto et al., 2007, 2008). The transformation of ANPP enables us to evaluate the relations between SQI and ANPP in the different LUCs in the same units.

3.3. Relation between SQI and ANPP

To evaluate the magnitude of the ecosystem response to LUC, we used a change detection technique based on the trajectories of the two biophysical indicators, i.e., the scores of SQI and ANPP. Each measurement of these indicators is represented by a point in a two-dimensional phase space. It produces two outputs – change magnitude and change direction. As illustrated in Fig. 2, the magnitude of the change (ΔMG) is computed by the Euclidean distance of a vector between the indicators, the initial (reference) state (S_1) and the observation (target) state (S_2):

$$\Delta \mathrm{MG} = \sqrt{(\mathrm{SQI1}_{S_1} - \mathrm{ANPP1}_{S_1})^2 + (\mathrm{SQI2}_{S_2} - \mathrm{ANPP2}_{S_2})^2} \tag{3}$$

A threshold, in terms of 1 standard deviation from the mean of the change, is defined for the magnitude values to distinguish between changed and unchanged trends. The direction of the change is computed by the angle (θ) of the change vector (Eq. 4):

$$\tan\theta = \frac{\mathrm{ANPP2}_{S2} - \mathrm{ANPP1}_{S1}}{\mathrm{SQI2}_{S2} - \mathrm{SQI1}_{S1}} \tag{4}$$

Due to its two output products, change magnitude and direction, this procedure enables us to quantify the different trajectories for the four LUCs and their ecosystem responses.

3.4. Statistical analyses

Analyses of variances for all parameters were tested using: (1) a General Linear Model (GLM) analysis of random effect (nested analysis of variance (AVOVA)); and (2) a one-way ANOVA for the average for each replicate ($n = 35$) and the separation of means was subjected to a Tukey test for significant difference. A Pearson correlation coefficients analysis was conducted to identify relationships between the measured soil properties. The statistical analysis was performed with STATISTICA Version 10, 2011 software. The soil quality transformation and indices (PCA, regression equations, scoring functions) were performed in MATLAB Version 7, 2011 software with a PLS toolbox (EIGENVACTOR research) and using Microsoft Excel packages. Soil quality indicators, soil quality indices, and primary productivity were tested for their level of significance at $p = 0.05$ between treatments.

4. Results

4.1. Soil quality

Table 1 shows the result of the LUC from a grazing system to a natural system (excluding grazing) on the north- and south-facing slopes for the physical, biological, and chemical soil properties. The transition from a grazing to a natural system showed significant differences between treatments in most of the soil properties, except root health, NO_3^-, and silt content. These differences are a combination of aspect and management effects. The results of the transition from a grazing system on the north- and south-facing slopes to a natural system show significant increases in the SH, PAC, pH, and potassium (Table 1). Additionally, a significant reduction in HC was observed in both slopes. However, the NH_4^+ and NO_3^- did not respond to the transition from a grazing to a natural system. These results of NH_4^+ and NO_3 are consistent with previous studies (Rietkerk et al., 2000; Lin et al., 2010; Segoli et al., 2012b). In addition, the results show that the south-facing slope has significantly lower NH_4^+, potassium, and EC values than the north-facing slope.

The supplementary data 2 represents the Pearson correlation coefficients for the measured soil quality properties in the grazing system. The soil properties interacted among themselves. Soil properties with significant correlations ($R \geq 0.5$) or with high coefficient correlations ($R \geq 0.8$) are marked in bold in the supplementary data 2. The SH and HC show a high negative Pearson correlation ($R = -0.81$).

Table 2 shows the results of the LUC in the different treatments in the agricultural systems for the physical, biological, and chemical soil properties. There are significant differences between all treatments in most of the soil properties, except for root health and silt content. In the transition from a natural to a grazing treatment, the results show significant increases in AWC, SOM, EC, NO_3^-, and potassium. On the other hand, significant reductions in the soil indicators NH_4^+ and pH were found in the grazing treatment. In the transition from the agricultural to the natural treatment, significant increases in AGG, SH, and potassium was observed. On the other hand, significant reductions in the soil properties of AWC, HC, NH_4^+, and NO_3^- were found from the agricultural to the natural treatment. In the transition from the agricultural to the grazing treatment, the results show significant increases in the soil properties of AWC, SH, SOM, EC, potassium, and phosphorus. On the other hand, significant reductions in HC, PAC, pH, and NH_4^+ were observed.

Table 1
Soil quality properties for the grazing system: northern and southern slope with grazing and no grazing treatments. Statistics include average value, standard deviation, and significant differences between treatments (small superscript letters).

Treatments	Sand (%)	Silt (%)	Clay (%)	AGG (1–6)	AWC (m/m)	SH (psi)	HC (mm/h)	SOM (%)	PAC (ppm)	RH (1–9)	pH	EC (dS/m)	$N(NH_4)$ (mg/kg)	$N(NO_3)$ (ml/kg)	P (mg/kg)	K (mg/kg)
Natural system No grazing northern slope	35.87 $\pm 2.22^a$	48.38 $\pm 1.41^a$	15.75 $\pm 0.96^a$	4.21 $\pm 0.33^b$	1.31 $\pm 0.13^a$	295.78 $\pm 10.41^a$	0.14 $\pm 0.04^c$	6.43 $\pm 0.51^{ab}$	597.92 $\pm 75.77^a$	1.23 $\pm 0.44^a$	7.088 $\pm 0.11^a$	0.858 $\pm 0.12^a$	71.72 $\pm 11.06^a$	8.465 $\pm 3.05^a$	14.18 $\pm 6.53^a$	10.96 $\pm 2.65^a$
Grazing system Grazing northern slope	34.74 $\pm 1.59^a$	47.68 $\pm 0.99^a$	17.57 $\pm 2.58^{ab}$	4.63 $\pm 0.34^a$	1.23 $\pm 0.12^a$	279.06 $\pm 16.2^b$	0.34 $\pm 0.04^a$	5.81 $\pm 0.83^b$	460.87 $\pm 60.1^b$	2.25 $\pm 0.58^a$	6.95 $\pm 0.09^b$	0.82 $\pm 0.09^a$	79.61 $\pm 11.36^a$	10.36 $\pm 4.59^a$	8.25 $\pm 3.5^b$	9.06 $\pm 2.31^a$
Natural system No grazing southern slope	31.34 $\pm 0.95^b$	49.46 $\pm 25.5^a$	19.20 $\pm 2.16^b$	4.76 $\pm 0.22^a$	1.36 $\pm 0.16^a$	288.89 $\pm 13.54^a$	0.08 $\pm 0.016^c$	6.59 $\pm 0.62^a$	588.09 $\pm 64.1^a$	1.7 $\pm 0.4^a$	7.02 $\pm 0.06^a$	0.66 $\pm 0.04^b$	57.51 $\pm 11.03^b$	8.14 $\pm 1.88^a$	11.01 $\pm 3.16^a$	8.71 $\pm 1.03^b$
Grazing system Grazing southern slope	33.62 $\pm 2.24^{ab}$	46.98^a ± 2.30	19.40 $\pm 0.89^b$	4.75 $\pm 0.26^a$	1.05 $\pm 0.19^b$	244.35 $\pm 29.27^b$	0.21 $\pm 0.03^b$	6.01 $\pm 0.97^b$	466.65 $\pm 82.01^b$	2.75 $\pm 0.55^a$	6.97 $\pm 0.05^b$	0.68 $\pm 0.05^b$	51.39 $\pm 9.28^b$	8.26 $\pm 1.54^a$	8.69 $\pm 3.1^b$	7.96 $\pm 1.41^b$
$p < \alpha$	<0.01	NS	<0.01	<0.01	<0.05	<0.01	<0.01	<0.01	<0.01	NS	<0.01	<0.05	<0.01	NS	<0.05	<0.01

AGG, aggregation; AWC, available water content; SH, surface hardness (penetration); HC, hydraulic conductivity (infiltration); SOM, soil organic matter; PAC, potential active carbon; RH, root health; EC, electrical conductivity; NH_4, ammonium; NO_3, nitrate; K, potassium; P, phosphorus; NS, no significant differences.

Table 2
Soil quality properties for the agricultural ecosystem: natural, agro, and grazing systems. Statistics include: average value, standard deviation, and significant differences between treatments (small superscript letters).

Treatments	Sand (%)	Silt (%)	Clay (%)	AGG (1–6)	AWC (m/m)	SH (psi)	HC (mm/h)	SOM (%)	PAC (ppm)	RH (1–9)	pH	EC (dS/m)	$N(NH_4)$ (mg/kg)	$N(NO_3)$ (mi/kg)	P (mg/kg)	K (mg/kg)
Natural system abandoned field no grazing	49.12 $\pm1.34^{a}$	37.08 $\pm1.09^{a}$	13.8 $\pm0.44^{c}$	2.87 $\pm0.19^{a}$	2.29 $\pm0.16^{c}$	311.9 $\pm4.16^{a}$	0.14 $\pm0.05^{b}$	3.96 $\pm1.05^{b}$	545.92 $\pm60.2^{a}$	2.1 $\pm0.31^{a}$	7.14 $\pm0.08^{a}$	0.73 $\pm0.12^{b}$	26.4 $\pm10.79^{b}$	8.68 $\pm6.03^{b}$	8.72 $\pm3.35^{ab}$	16.93 $\pm3.01^{b}$
Agro system	44.32 $\pm1.14^{b}$	38.68 $\pm1.95^{a}$	17.0 $\pm1.01^{b}$	2.33 $\pm0.21^{b}$	2.62 $\pm0.06^{b}$	265.89 $\pm12.9^{b}$	0.58 $\pm0.07^{a}$	3.21 $\pm0.14^{b}$	564.55 $\pm64.2^{a}$	2.3 $\pm0.47^{a}$	7.06 $\pm0.09^{a}$	0.89 $\pm0.12^{b}$	43.188 $\pm10.1^{a}$	31.43 $\pm11.7^{a}$	8.14 $\pm1.47^{b}$	10.63 $\pm6.52^{c}$
Grazing system abandoned field with grazing	39.52 $\pm4.15^{c}$	38.08 $\pm3.11^{a}$	22.4 $\pm2.88^{a}$	2.77 $\pm0.26^{a}$	3.18 $\pm0.19^{a}$	306.182 $\pm8.43^{a}$	0.22 $\pm0.07^{b}$	7.38 $\pm1.21^{a}$	456.52 $\pm53.2^{b}$	2.7 $\pm0.47^{a}$	7.01 $\pm0.1^{b}$	1.04 $\pm0.114^{a}$	17.73 $\pm9.68^{c}$	24.63 $\pm7.93^{a}$	14.2 $\pm4.52^{a}$	34.72 $\pm11.26^{a}$
$p < \alpha$	<0.01	NS	<0.01	<0.01	<0.05	<0.01	<0.01	<0.01	<0.01	NS	<0.01	<0.01	<0.05	<0.01	<0.01	<0.01

AGG, aggregation; AWC, available water content; SH, surface hardness (penetration); HC, hydraulic conductivity (infiltration); SOM, soil organic matter; PAC, potential active carbon; RH, root health; EC, electrical conductivity; NH_4, ammonium; NO_3, nitrate; K-potassium; P, phosphorus; NS, no significant differences.

The supplementary data 3 represents the Pearson correlation coefficients for the measured soil properties in the agricultural system. The results that represent soil properties with significant correlations ($R \geq 0.5$) or with high coefficient correlations ($R \geq 0.8$) are marked in bold. A positive correlation was found between AWC and SH.

The radar diagrams in Fig. 4 demonstrate the soil quality scoring (normalized between 0 and 1) of the different soil properties. The radar diagrams impress the soil quality scoring values. The enveloping lines represent the soil treatments, enabling us to compare among them with respect to each soil property. Fig. 4A shows the changes in most of the soil properties (not including texture) in the grazing system. The results show that grazing in both slopes changes most of the biological indicator's lines toward the origin, therefore resulting low quality. On the other hand, the physical indicator's lines against the origin display higher soil quality in the grazing treatments in both slopes. The soil trampling causes changes in the SH and HC. The radar diagram in Fig. 4B shows the changes in the quality for each soil property in the agricultural system. The results show that the natural system has higher soil quality values in AWC, HC, AGG, and phosphorus.

4.2. Integration into soil quality index

The indices were developed from the results of the transformed scoring of soil properties for the LUCs. In the grazing system, the RH and the NO_3^- did not show significant differences between treatments; therefore, they were excluded from the PCA (Table 1). The first three PCs had eigenvalues > 1 and were included in the PCA with a total cumulative variance of 79.6% in PC 1-3 (Table 3). The highly weighted variables under PC-1 were AWC, SH, SOM, PAC, NH_4^+, pH, EC, phosphorus, and potassium. AGG had the highest weighted variables under PC-2. HC had the highest weighted variables under PC-3. Weights for selected soil properties were determined by the percentage of variation in the dataset explained by the first three PCs. Soil quality was calculated using a weighing factor for each, scoring soil properties according to Eq. (2). The SQI results of the grazing system are presented in Fig. 5, stratified by the physical, biological, and chemical soil properties. The scores of the SQI in the grazing system in the north- and south-facing slopes are 0.61 and 0.54, respectively. The scores of the SQI with no grazing in the north- and south-facing slopes are 0.70 and 0.67, respectively, and are significantly higher than the grazing land-use ($F_{(3,76)} = 21.55$; $p \leq 0.01$).

In the agricultural system, the RH did not show significant differences between treatments; therefore, it was not included in the PCA (Table 2). The first three PCs had eigenvalues > 1 and were included in the PCA that resulted in a cumulative variance of 76.14% in PC 1-3 (Table 4). The highly weighted variables under PC-1 were AGG, AWC, SH, PAC, NH_4^+, pH, NO_3^-, and potassium. The transformed data in PC-1 were correlated between themselves in the SH and AWC with a high correlation coefficient ($R = 0.8$); therefore, the AWC was excluded from SQI (supplementary data 3). The weight for AWC was decided as factor loadings. Phosphorus had the highest weighted variables under PC-2, while SOM, HC, and EC had the highest weighted variables under PC-3. As before, the transformed data in PC-2-3 were not correlated among themselves and were all included in the PCA. Weights for selected soil properties were determined by the percentage of variation in the dataset explained by the first three PCs. The SQI results of the agricultural system are presented in Fig. 5, stratified by the physical, biological, and chemical soil properties. The natural system score is 0.66. The score of the wheat field (agro-system) is 0.67. The grazing system score is 0.54 and is significantly lower than the natural and agro system ($F_{(2,57)} = 68.21$; $p \leq 0.01$).

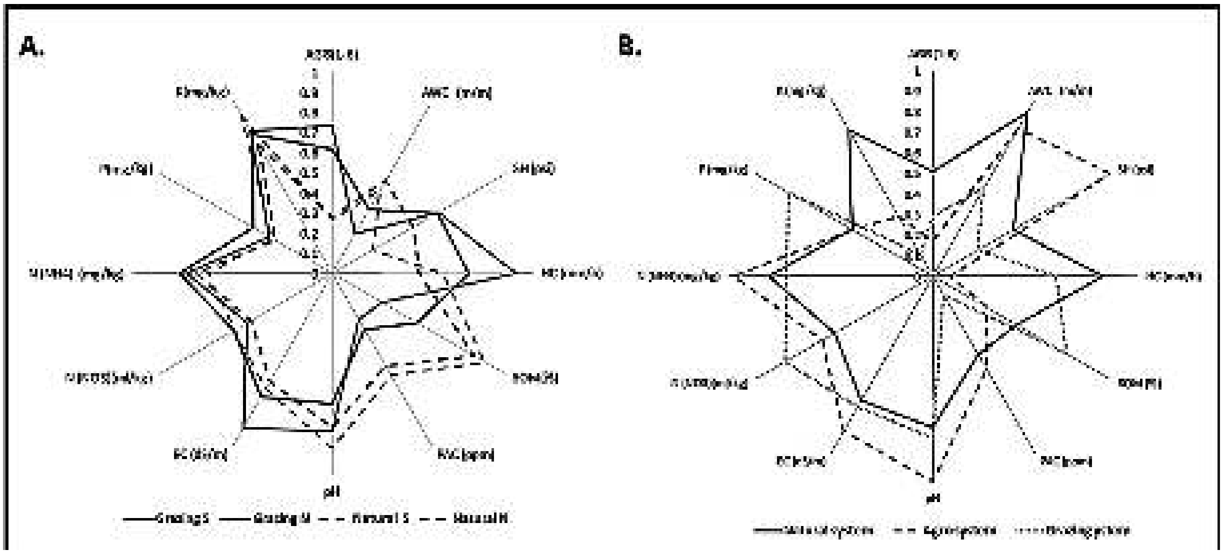

Fig. 4. Radar plot of soil quality index scoring normalized between 0 and 1: (A) a grazing system with different treatments (south- and north-facing slopes of natural and grazing systems); (B) an agricultural system with different treatments (natural, grazing, and agro-systems). AGG, aggregation; AWC, available water content; SH, surface hardness (penetration); HC, hydraulic conductivity (infiltration); SOM, soil organic matter; PAC, potential active carbon; RH, root health; EC, electric conductivity; NH_4, ammonium; NO_3, nitrate; K, potassium; P, phosphorus; NS, no significant differences.

Table 3
Results of principal component (PC) analysis of soil properties in the grazing system. Bold values indicate eigenvalues, variance, and cumulative variance corresponding to the PCs examined for the index. Bold and underlined values indicate underlined factors corresponding to the indicators included in the indices. Bold values indicate high multivariate correlations under a single PC that were, therefore, eliminated from the SQI.

	Scores on PC 1 (48.14%)	Scores on PC 2 (17.47%)	Scores on PC 3 (13.53%)
Eigenvalue	3.85	1.39	1.08
Variance	48.14	17.33	13.53
Cumulative variance	48.14	64.47	79.6
AGG (1–6)	2.11	**5.32**	−3.46
AWC (m/m)	**−3.35**	0.36	−1.69
SH (psi)	**7.58**	−5.48	−6.89
HC (mm/h)	1.55	−3.69	**7.07**
SOM (%)	**−7.62**	1.01	−0.77
PAC (ppm)	**−6.05**	2.72	0.79
pH	**−6.12**	0.13	0.11
EC (dS/m)	**9.21**	2.51	3.02
NH_4^+ (ppm)	**−7.32**	1.02	0.42
K (mg/kg)	**−5.16**	−0.77	0.97
P (mg/kg)	**8.32**	1.15	2.02

AGG, aggregation; AWC, available water content; SH, surface hardness (penetration); HC, hydraulic conductivity (infiltration); SOM, soil organic matter; PAC, potential active carbon; RH, root health; EC, electrical conductivity; NH_4, ammonium; NH_3, nitrate, K, potassium; and P, phosphorus.

Table 4
Results of principal component (PC) analysis of soil properties in the agricultural system. Bold values indicate eigenvalues, variance, and cumulative variance corresponding to the PCs examined for the index. Bold and underlined values indicate underlined factors corresponding to the indicators included in the indices. Bold values indicate high multivariate correlations under a single PC that were, therefore, eliminated from the SQI.

	Scores on PC 1 (40.88%)	Scores on PC 2 (19.26%)	Scores on PC 3 (16.29%)
Eigenvalue	2.45	1.16	1.01
Variance	40.88	19.26	16.29
Cumulative variance	40.88	60.14	76.14
AGG (1–6)	**−7.45**	−2.4	0.01
AWC (m/m)	**4.03**	−1.9	2.02
SH (psi)	**4.87**	3.68	4.29
HC (mm/h)	−3.9	4.19	**−4.85**
SOM (%)	−0.89	−3.09	**−4.60**
PAC(ppm)	**−6.15**	−1.20	4.65
pH	**5.90**	4.51	−1.66
EC (dS/m)	3.07	0.09	**3.105**
NH_4^+ (mg/kg)	**3.01**	−1.16	0.67
NO_3^- (mg/kg)	**4.80**	−3.28	1.28
K (mg/kg)	−0.69	**−4.29**	−0.64
P (mg/kg)	**−6.57**	4.95	1.94

AGG, aggregation; AWC, available water content; SH, surface hardness (penetration); HC, hydraulic conductivity (infiltration); SOM, soil organic matter; PAC, potential active carbon; RH, root health; EC, electrical conductivity; NH_4, ammonium; NH_3, nitrate, K, potassium; and P, phosphorus.

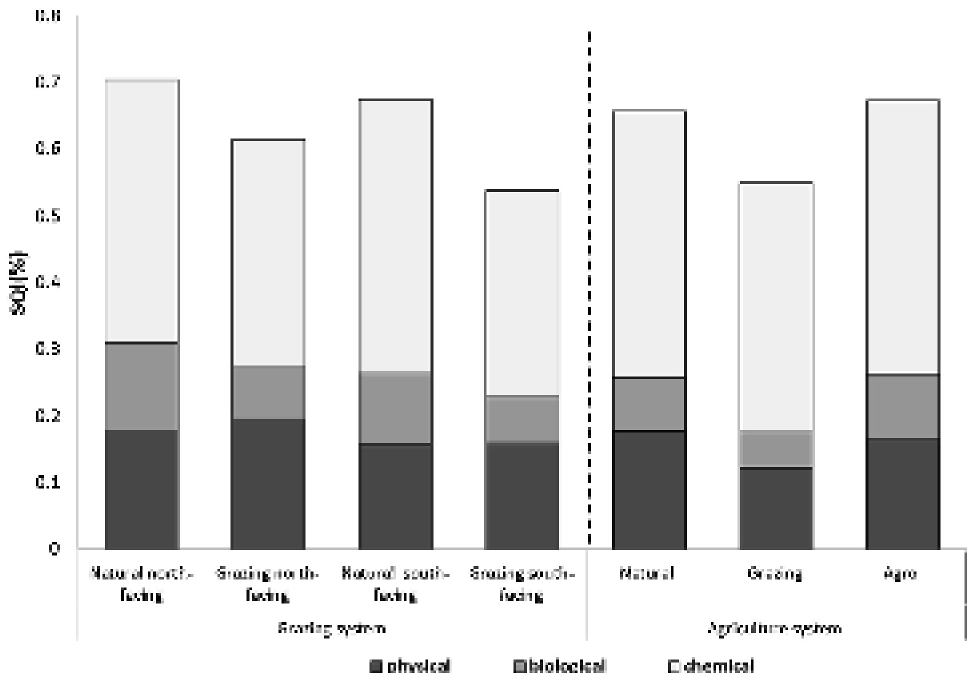

Fig. 5. Soil quality index (SQI) in the grazing and agricultural systems by the physical, chemical and biological scoring transformed data. The evaluation of the four transitions in the semi-arid area: transitions from a grazing to a natural system in the north- and south-facing slope; transitions from a natural system to a grazing system; transitions from an agro-system to a natural system; and transitions from an agro-system to a grazing system.

4.3. Aboveground net primary productivity

The results of the aboveground herbaceous biomass in the grazing and agricultural systems show significant differences ($F_{(3,180)} = 45.37$; $p < 0.01$ and $F_{(2,135)} = 55.5$; $p < 0.01$, respectively) between the LUCs (Fig. 6). Significantly higher ANPP was found in the natural system in the north-facing slope in all years (2010–2012) than in the grazing system (from an average for all year's ANPP of 323.5–201.3 mg/m^2, respectively). In the natural system, on the south-facing slope, significantly higher biomass was found than in the grazing system only in the year 2010. No significant change was found in the years 2011–2012 (from an average for all year's ANPP of 206.7–160.9 mg/m^2, respectively). Additionally, significant differences were found between the south- and north-facing slopes.

In the transition from the agro- to the natural system, no significant differences were found in ANPP in the years 2010–2012 (from an average for all years of 300.1–280.3 mg/m^2, respectively). In the transition from the natural to the grazing system, significant differences were found in the ANPP in the years 2010–2012 (from an average for all years of 280.3–164.4 mg/m^2, respectively). In the transition from the agro- to the grazing system, significant differences were found in the ANPP in the years 2010–2012 (from an average for all years of 300.1–164.4 mg/m^2, respectively).

4.4. Correlation between SQI and ANPP

The scatter plot in Fig. 7 demonstrates the correlation between the transformed SQI and ANPP results in the different LUCs. A significant correlation between SQI and ANPP was found in the grazing system ($R^2 = 0.70$; $p < 0.05$) in the north- and south-facing slopes (Fig. 7A). Additionally, in the agricultural system, a significant correlation between SQI and ANPP was found ($R^2 = 0.85$; $p < 0.05$) (Fig. 7B). The transition from the grazing to the natural system caused an improvement in SQI and ANPP (Fig. 7A–B). In the agricultural system, the transition from the natural and the agro-system to the grazing system caused a reduction in SQI and ANPP (Fig. 7B). The transition from an agro-system to a natural system showed no significant differences.

5. Discussion

Ecosystem responses to LUC occur worldwide over a wide range of spatial and temporal scales (DeFries et al., 2004; Cardille and Lambois, 2009). Several studies have suggested that in the large scale, the LUC of natural systems to human-controlled ecosystems generated a new era, the Anthropocene, in which human beings are changing the earth system (Steffen et al., 2007). Traditionally, studies in ecosystem science have emphasized alternation and state change in natural ecosystems (Pickett and Cadenasso, 1995). Given the important role that LUC by humans plays in the modulation of the biosphere, ecosystem science should shift its focus from alternation within natural ecosystems to transitions between ecosystems. Ecosystem responses to LUC include biological diversity and biogeochemical, hydrological, and climatic responses that are linked (DeFries et al., 2004; Potschin, 2009). To cope with the suggested paradigm shift in ecosystem studies, we constructed an ecosystem-response-to-LUC framework that incorporates changes both in the soil state (soil quality) and the vegetation state (net primary production) in order to portray LUC dynamics (Figs. 1 and 2).

5.1. Ecosystem responses to land-use change (LUC) in the Negev

Fig. 8 summarizes ecosystem responses to LUC in the Negev using the integrated SQI and ANPP trajectories. In all the transitions, the trajectories show an increase or decrease in both SQI and ANNP, indicating a high correlation and significant relationships between soil and vegetation states (e.g. Masto et al., 2008). In our study, in the transitions from a grazing to a natural system did the trajectories show an increase in both SQI and ANNP, which indicates improvements in both soil and vegetation states as the first hypothesis suggests. This general trend was similar for both north- and south-facing slopes. However, they differed in the magnitude

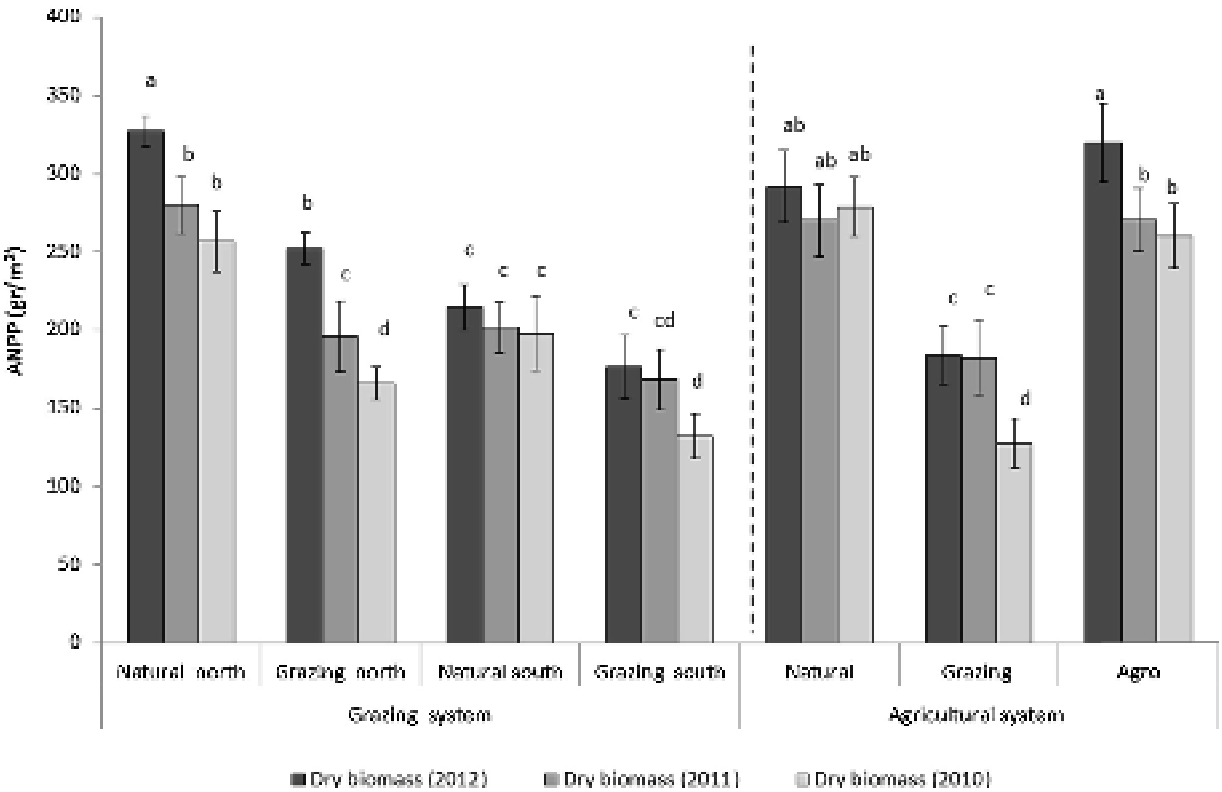

Fig. 6. The results of the aboveground net primary productivity in the grazing and agricultural systems, average biomass measurements and standard deviations for the years 2010–2012. Small letters represent significant differences between treatments in the different years and between etch treatment. The evaluation of the four transitions in the semi-arid area: transitions from a grazing to a natural system in the north- and south-facing slope; transitions from a natural to a grazing system; transitions from an agro-system to a natural system; and transitions from an agro-system to a grazing system.

(0.47 for the north and 0.2 for the south) and the direction of the change of angle (77° for north and 42° for south). The observed general trend indicates that long-term (ca. 10,000 years) (Perevolotsky, 1995) traditional grazing negatively affects both ANPP and SQI (Goudie, 2009). We assume that the actual magnitude of reduction in both soil and vegetation states in the long-term transition from a natural to a grazing system is higher than our measured recovery magnitudes (0.47 for the north and 0.2 for the south). This assumption is supported by reports on grazing-induced desertification, i.e., deterioration in the soil and vegetation states in response to grazing (Asner et al., 2004). Excluding grazing from the system for a short period (ca. 20 years) enables the development of a new plant community, dominated by a highly productive annual plant species that increases primary production (Osem et al., 2004). In addition, excluding grazing reduces trampling and enables biological soil crust recovery (Zaady et al., 2001).

We attribute the high rate of changes in both vegetation and soil states during the ecosystem response to LUC from grazing to natural ecosystems to the ecological properties of the plant and soil crust communities. The dominant plant community in the study area is of herbaceous annual plants. This community is highly diverse with about 130 species and functionality in relation to ANPP (Osem et al., 2002). Individual plant ANPP ranges from 0.005–0.275 g per a year (Osem et al., 2002). When grazing is excluded, the pressure on the individuals of highly productive species is reduced, and they increase their abundance by seed dispersal or from the available seed bank (Osem et al., 2006; Maestre et al., 2012; Segoli et al., 2012a) in a relatively short time. The net effect of the annual plant community's high rate of re-organization is an increase in total ANPP in a short period (Fig. 6) by rapid recovery of the plant community. In addition, the high colonization rate (between 10 and 20 years) (Shachak and Lovett, 1998) of the cyanobacteria results in a high recovery of a functional biological soil crust that generates surface runoff, consequently enhancing the creation of water-enriched patches (Shachak et al., 1998; Cuddington et al., 2007). We propose that the combined effect of the above two fast processes is responsible for changes in the vegetation and soil states in the ecosystem response to LUC from a grazing to a natural system.

Different trends were obtained in the phase plane in cases in which the initial state before transition was an agricultural system. All transitions that started from agricultural systems and moved toward less intensively managed systems, such as grazing or natural systems, showed no significant changes or decreases in either the vegetation or the soil state (MG = 0.12 and $\theta = 230°$ for agro- to natural system with no significant change, and MG = 0.57and $\theta = 264°$ for agro- to grazing system (Fig. 8(). Our results are not compatible with our hypothesis and other findings that showed that the transition from an agricultural to a natural ecosystem increases both ANPP and SQI (e.g. Swift et al., 2004; Clergue et al., 2009; Idowu et al., 2009; Smith et al., 2012). In the transition from an agro- to a natural system, no significant changes were found in the trajectories of SQI and ANPP. In order to rehabilitate natural systems, species from adjacent natural systems have to disperse and re-colonize the formerly agricultural system. Colonization by highly productive species can increase the total ANPP, as well as the complementary use of resources by high species diversity. A high species diversity that includes highly productive species depends on the species pool size and composition in the vicinity of the abandoned agricultural system (Flinn and Vellend, 2005). These conditions did not exist in our case since the system is surrounded by intensive agricultural fields. In the short-term, the surround endearment of intensive agricultural fields may influence the ability of the natural system to recover after agricultural abandonment.

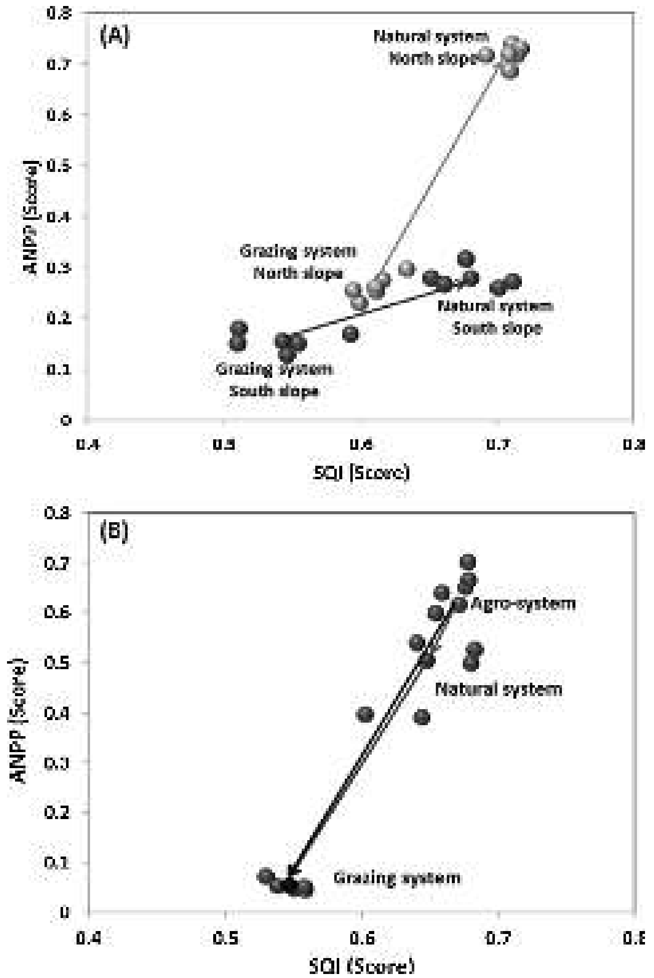

Fig. 7. The scatterplot of soil quality index scoring and aboveground net primary productivity scoring in the grazing, agricultural, and natural systems. The evaluation of the four land-use transitions in the semi-arid area: (A) grazing system and (B) agricultural system. Colored points represent average values of the replication in each treatment.

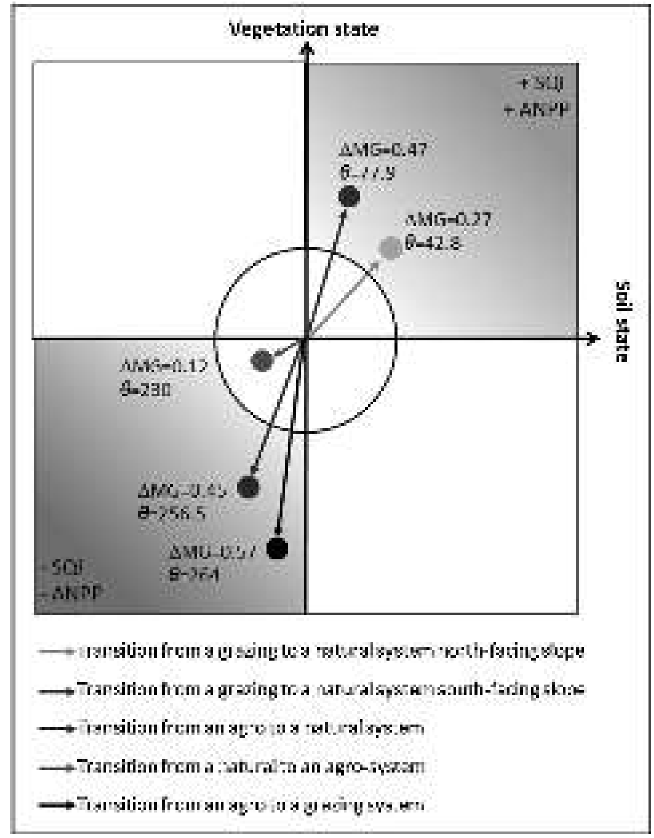

Fig. 8. Ecosystem responses to land-use changes evaluated by soil quality and aboveground net primary productivity changes in the Negev. The arrows point to the direction of change, the length of the arrow indicates the magnitude (MG) of change and slope angle (θ) represents the relative changes in the vegetation and soil states.

A significant reduction in SQI and ANPP in the phase plane (MG = 0.45; $\theta = 256^{\circ}$) was found in the transition from an agriculture to a grazing system. In this transition, the dominant plant of wheat was replaced by the native species of *Sinapis alba* L. that has a lower productivity than wheat per an area. In addition to this, the species pools from adjacent natural systems haven't dispersed and re-colonized in this system. Colonization by a low productive species, such as *Sinapis alba* L., can reduce the total ANPP, as well as the complementary use of resources by low species diversity. Moreover, the reduction in the SQI was caused by soil compaction that included an increase in the surface hardeners (SH) and a reduction in water infiltration and hydraulic conductivity (HC). The transition from an agricultural to a grazing system is expressed in a high change in soil compaction (Table 2), due to the cessation of cultivation and the initiation of livestock introduction. In this case, grazing affected water flow (low HC) in the system through the trampling of livestock that caused soil compaction (Zaady et al., 1998; Eldridge et al., 2000). Soil compaction affects the re-colonization of species by reducing the ability of seeds to penetrate the soil surface (Boeken and Shachak, 2006).

In the transition from a natural system to a grazing system, where the initial state was agricultural use, we identified reductions in the soil and vegetation phase planes (MG = 0.57; $\theta = 264^{\circ}$ respectively). Our results are compatible with our fourth hypothesis that grazing reduces the trajectories of SQI and ANPP. This is due to the introduction of livestock to a natural system, which increases resource uptake and soil degradation (Fleischner, 1994). However, since the initial state of the natural system was agricultural, additional effects, such as species colonization rate, species production, and species pool size and composition in the vicinity of the abandoned agricultural system, must be considered, as mentioned above.

5.2. Developing a framework of ecosystem response to LUC

LUC processes have profound implications for ecological studies and, specifically, for the advancement of ecosystem science in the human-controlled biosphere (Foley et al., 2005). Now that ecologists more widely investigate ecosystems as socio-ecological systems (Daily et al., 1997; Vitousek et al., 1997; Rodríguez et al., 2006; Swinton et al., 2007), ecosystem concepts could be integrated into a framework that addresses the general features of ecosystem response to LUC processes. This implies that ecosystem science should provide tools for the developing LUC theoretical and practical framework to quantify changes in ecosystem function at any transition. To our knowledge, the linkage of ecosystem science and LUC in a theoretical framework that could enhance field work for a deeper understanding of LUC and ecosystem response is still lacking. Our work is an attempt to incorporate elements from ecosystem science, using two universal terrestrial ecosystem properties, SQI and ANPP, into LUC processes (Foley et al., 2005). In our framework, the trajectories of variables that indicate changes in soil and vegetation states are used to indicate the changes of terrestrial ecosystem components (soil and vegetation) in response to LUC (Fig. 2). In addition, the use of SQI and ANPP as indicators for evaluating ecosystems response to LUC can be assessed by other methods such as remote sensing and spectroscopy (e.g. Tucker, 1980; Huete, 1988; Qi et al., 1994; Running et al., 1995; Ben-Dor et al., 2009). The use of remote sensing can improve the ability of monitoring large areas in different time scale. However, the challenge is to adapt remote sensing application toward a diagnostic screening tool that can aid the development of reliable specific spectral definitions to characterize soil quality and plant productivity for regional environmental management. Testing the framework in the Negev case study revealed four properties of the framework that can be used for developing a science of LUC:

(1) *Comparison between different types of transitions:* The science of LUC needs to integrate operational and universal ecosystem responses to allow comparisons of the changes in ecological attributes for any LUC using empirical studies. Our framework suggests that SQI and ANPP are good ecological indicators that can be used to compare changes in six basic LUCs (Figs. 1 and 2). We generated comparable trajectories in relation to the direction and the magnitude of SQI and ANPP in a phase plane (Fig. 8) for the four LUC in the Negev Desert. The trajectories depict a variety of transitions, from managed systems to self-organized ecosystems and vice versa. In addition, the trajectories manifest local differences, such as north- and south-facing slopes and management intensity. Therefore, we propose that the SQI and ANPP trajectories, as a theoretical framework, can be used as a foundation for developing the science of ecosystem response to LUC. However, the validity and the generality of the framework should be tested over a wide range of LUCs in terrestrial systems around the world.

(2) *Land-use changes between self-organized and managed systems:* LUC attributes are strongly affected by the transition between self-organized and imposed processes (Rietkerk et al., 2004). LUC from a natural ecosystem to a grazing or agro-ecosystem can be described as the imposed engineering of a new ecosystem that re-designs systems. LUC from grazing or agro systems-to natural ecosystems can be viewed as a release of the engineering constraints, which enables the system to re-organize itself through self-organized processes. All LUCs in terrestrial ecosystems consist of one of the following: re-designing of self-organized systems by management, the re-designing of managed systems or re-organization by self-organized processes. The four LUCs in our study represent the principle movements among re-designed and self-organized systems. We were able to detect the ecosystem consequences of the movements between re-designed and self-organized systems using the SQI and ANPP trajectory framework. Analysis of the trajectories showed, for example, that transitions from managed to self-organized systems can have either a positive effect or no effect on the SQI and ANPP trajectories, while the engineering of a transition from a self-organized natural ecosystem to a grazing ecosystem shows a negative effect (Fig. 8). The ability of the SQI and ANPP trajectory framework to depict the most fundamental properties of ecosystem response to LUC, i.e., a reduction or an increase in bottom-up self-organization control or top-down human management control, suggests its potential as an essential element for establishing an LUC science.

(3) *Identification of short- and long-term effects:* Land-use change science needs to draw on indicators that measure both “slow” and “fast” variables that signify short- and long-term effects on ecosystem structure and function. The SQI and ANPP trajectory framework proposes that the essential change of a given ecosystem can be captured by including key soil and vegetation states with long or short time scales. In the framework, soil quality depicts the net effect of slow physical, chemical and biological processes that determine soil control over ecosystem response to LUC, while ANPP represents a faster response to LUC. Our study focuses on soil and vegetation responses on a short to intermediate time scale (ca. 20 years). Over this time scale, we identified changes in both SQI and ANPP that represent the effects of slow and fast variables, respectively. If future studies show that SQI and ANPP trajectories represent the effect of slow and fast variables over a range of time scales, this will strengthen the role of SQI and ANPP trajectories in the developing of an LUC science.

(4) *Integration of biodiversity and ecosystem function:* The functioning of ecosystems is affected by changes in biodiversity, of which LUC is an important driver (Gaston, 2000; Sala et al., 2000; Schwartz et al., 2000; Maestas and Gilgert, 2003). Consistent shifts in plant functional composition and diversity as a consequence of LUC can trigger cascading direct, indirect, and interactive effects on multiple ecosystem functions (Sala et al., 2000; Hooper et al., 2005; Srivastava and Vellend, 2005; Hillebrand and Matthiessen, 2009). This suggests that changes in biodiversity may be one way through which changes in land use alter ecosystem functioning and responses. In our framework, the extent to which changes in plant diversity translates into changes in ecosystem functioning is expected to be expressed by SQI and ANPP trajectories. The relationships among SQI, ANPP and biodiversity are complex (Cottingham et al., 2001; Loreau et al., 2001; Costanza et al., 2007; Hillebrand and Matthiessen, 2009). Soil quality can exert dominant control over ANPP, both directly via resource availability to plants (Burke et al., 1997; Lambers et al., 2008) and indirectly via shifts in plant functional composition. Soil quality index and ANPP are, therefore, key controllers of plant diversity (Huston, 1994), which, in turn, affects SQI and ANPP. We explain our results that showed changes in SQI and ANPP in the Negev by shifts in plant functional composition and diversity, with cascading effects on multiple ecosystem functions, such as production and decomposition. We assume that in our case, changes in SQI and ANPP were probably caused by changes in the plant community resource uptake capability (Burke et al., 1997; Lambers et al., 2008) as a consequence of a shift in plant diversity during LUC. In our study, we did not investigate the relations among SQI, ANPP and biodiversity. However, we assume that changes in the various dimensions of biodiversity are the mechanism that drives the observed SQI and ANPP trajectories. In conclusion, we see two possibilities for integrating biodiversity dimensions within the science of LUC on ecosystem response: (1) to transfer the SQI and ANPP plane into a three-dimensional volume by adding a biodiversity axis that will represent the trajectories of SQI, ANPP and biodiversity; or (2) to treat biodiversity as an effect variable and the trajectories of SQI and ANPP as response variables.

6. Summary and conclusions

In this study, we suggest a framework for evaluating ecosystem response to LUC, by incorporating elements from ecosystem science using two universal terrestrial ecosystem indicators, SQI and ANPP, into LUC processes. In the framework, the trajectory of variables that indicate changes in soil and vegetation states are used to indicate the changes in terrestrial ecosystem components (soil and vegetation) in response to LUC. We evaluated the framework in four transitions in the Negev Desert as a case study. This enabled us to evaluate changes in the trajectories of the SQI and ANPP phase plane. We found that the relationships between SQI and ANPP in LUC are highly correlated and can be quantified by the magnitude and the change vector angle method. We suggest that the properties of the trajectories are highly dependent on the transition in species diversity and species traits, such as complementary resource use and high species production. However, future studies are needed. We suggest that changes in biodiversity may be one way through which changes in land use alter ecosystem functioning. In our framework, the extent to which changes in plant diversity translate into changes in ecosystem functioning is expected to be expressed by SQI and ANPP trajectories. The results of this study contain critical aspects at the regional scale for land-use management. In addition, we suggest that the framework could be reliable for evaluating ecosystem response to LUC in additional terrestrial systems in the world. The framework can be used for comparing between different types of transitions, identifying short-term changes and local factors in the dimensions of the LUC and comparing between self-organized and imposed processes. Adding the additional factor of biodiversity to the framework may improve the analysis of ecosystem response to LUC dynamics, but future studies are needed. Ecosystem responses to LUC processes have profound implications for ecological science and, specifically, for the advancement of ecosystem science in a human-controlled biosphere. Our framework could be integrated into an address the general features of LUC processes in this emerging science of ecosystem modification.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2014.04.024.

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